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Geographic origin and spread of cosmopolitan ants (Hymenoptera: Formicidae)

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Abstract

I have compiled a list of 42 "cosmopolitan" ant species, i.e., ants with multiple well-established populations in both the Old World and New World, spread through human commerce. Twenty of the 42 cosmopolitan ant species have established populations in all seven of the world's ant-inhabited biogeographic regions (i.e., all except the Antarctic): Afrotropic, Palearctic, Indomalay, Australasia, Oceania, Nearctic and Neotropic. Of the 42 cosmopolitan ant species, 35 (83%) are Old World natives and seven (17%) are New World natives. Cosmopolitan ant species are most often originally native to the Indomalay bioregion (17 species) and are least often native to the Nearctic bioregion (only one species). Only twelve cosmopolitan ants have become major ecological, agricultural, and/or household pest species: Anoplolepis gracilipes, Linepithema humile, Monomorium pharaonis, Nylanderia bourbonica, Paratrechina longicornis, Pheidole megacephala, Solenopsis geminata, Solenopsis invicta, Tapinoma melanocephalum, Technomyrmex difficilis, Trichomyrmex destructor, and Wasmannia auropunctata. The other 30 species are, at most, minor pests. Documenting the exotic spread of ant species within their own native hemisphere will be more complicated because it is often difficult to evaluate what geographic area constitutes the native range and what area, if any, constitutes the exotic range.

Key words: ants, exotic species, invasive species.

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Introduction

Numerous tramp ant species have been transported around the world, hidden in our plant products, packaging material, building supplies, and heavy machinery such as logging and military equipment. Some of these ant species have had great population explosions in areas they have invaded, causing serious ecological and economic problems. Other species have remained rare and/or inconspicuous and have had no discernable impact.

Forel (1911) compiled a list of ant species, spread by humans, which had achieved or were in the process of achieving broad cosmopolitan distributions in both the Old World and the New World (Table 1). Eight of these species are now global pests: Anoplolepis gracilipes (Smith, 1857), Linepithema humile (Mayr, 1868), Monomorium pharaonis (Linnaeus, 1758), Paratrechina longicornis (Latreille, 1802), Pheidole megacephala (Fabricius, 1793), Solenopsis geminata (Fabricius, 1804), Tapinoma melanocephalum (Fabricius, 1793), and Trichomyrmex destructor (Jerdon, 1851). Five others are widespread, but have not developed into major pests, with substantial ecological and/or economic impacts (see below): Cardiocondyla emeryi Forel, 1881, Monomorium floricola (Jerdon, 1851), Tetramorium bicarinatum (Nylander, 1846), Tetramorium lanuginosum Mayr, 1870, and Tetramorium simillimum (Smith, 1851), though in Forel's time, *Tetramorium "simillimum"* also encompassed a second distinct tramp species, Tetramorium caldarium (Roger, 1857). The last two species on Forel's list, Nylanderia vividula (Nylander, 1846) and Odontomachus haematodus (Linnaeus, 1758), may not be cosmopolitan tramps at all. Instead, in Forel's time these two names, each represented what are now recognized as several species with different regional ranges and whose taxonomic boundaries remain uncertain. After dropping N. vividula and O. haematodus, and adding T. caldarium to Forel's (1911) list, a striking trend

emerges: only two of these 14 cosmopolitan species are native to the New World: L. humile and S. geminata (Table 1).

Over the past century, many additional ant species, not on Forel's list, have achieved cosmopolitan distributions, with broad ranges in both the Old World and New World. In the present study, I evaluate the worldwide distribution of all ant species reported to have established populations outside their native hemisphere.

Methods

I compiled both published and unpublished site records for all ant species that have been reported as having exotic populations. I obtained unpublished site records from museum specimens in the collections of Archbold Biological Station, the Museum of Comparative Zoology, the Smithsonian Institution, and (for Forel's (1911) cosmopolitan species) the British Museum. In addition, I used online databases with collection information on specimens by Antweb (www.antweb.org), and the Global Biodiversity Information Facility (www.gbif.org). I also received unpublished collection information from numerous other researchers.

For analyzing the worldwide distributions of the ants, I categorized each site record as belonging to one of seven terrestrial biogeographic realms (following Olson et al., 2001; Old World = bioregions 1-5; New World = bioregions 6-7): 1) The Afrotropic bioregion (22.1 million km^2) includes sub-Saharan Africa, the southern and eastern coasts of the Arabian Peninsula, southern Iran, southwestern Pakistan, Madagascar, western Indian Ocean islands, Cape Verde, and southern mid-Atlantic islands. 2) The Palearctic bioregion (54.1 million km^2) includes Europe, northern Africa, Canary Islands, Madeira, northern and central Arabian Peninsula, and Asia north of the Himalayas, and the main islands of Japan. 3) The Indomalay bioregion (7.5 million km^2) includes southeastern Pakistan, the Indian subcontinent, Southeast Asia, southern China, Philippines, Taiwan, and Japan's Ryukyu Islands, and Indonesia west of Wallace's line. 4) The Australasia bioregion (7.6 million km^2) includes Australia, New Guinea, Indonesia east of Wallace's Line, Vanuatu, Solomon Islands, New Caledonia, and New Zealand. 5) The Oceania bioregion (1.0 million km^2) includes the Pacific islands of Fiji, Micronesia, and Polynesia (except New Zealand). 6) The Nearctic bioregion (22.9 million km^2) includes North America south to the Mexico highlands (except southern Florida), Bermuda, and Greenland. 7) The Neotropic bioregion (19.0 million km^2) includes South and Central America, south and central Mexican lowlands, Caribbean islands, southern Florida, and the Bahamas.

When an ant species occurs in both the Old World and the New World, it is almost always clear that one of these ranges is entirely exotic. Within a hemisphere, however, it is often much more difficult to evaluate what geographic area constitutes the native range and what area, in any, constitutes the exotic range. For this reason, when an ant has a fairly continuous distribution in its native hemisphere and I have no evidence to the contrary, I designated the entire continuous distribution as part of the native range, and listed the entire bioregion as native (Tables 1-4).

I defined a cosmopolitan ant as an ant species, with multiple well-established outdoor populations, outside their native hemisphere, spread through human commerce. Although in the tables I included indoor records for species with broad exotic ranges, I did not include species with records outside their native hemisphere known solely from indoors. I also have not included several ant taxa, with reports of spread outside their native hemisphere, whose worldwide status remains unclear due to taxonomic problems analogous to those of N. vividula and O. haematodus (see Introduction), and may represent multiple species, e.g., Brachymyrmex cordemoyi Forel, 1895, Brachymyrmex obscurior Forel, 1893, Camponotus herculeanus (Linnaeus, 1758), Lasius alienus (Foerster, 1850), Lasius flavus (Fabricius, 1782), Lasius niger (Linnaeus, 1758), Monomorium monomorium Bolton, 1987, Nylanderia vaga (Forel, 1901), Ochetellus glaber (Mayr, 1862), and Tetramorium caespitum (Linnaeus, 1758). I have also omitted several species whose extra-hemispheric records are all dubious, e.g., Pheidole anastasii cellarum

Forel, 1908 (= Pheidole bilimeki Mayr, 1870) (see Fischer and Fisher, 2013).

Results

My analyses distinguished 60 ant species with outdoor populations established outside their native range hemisphere (Tables 1-4). Of these, 42 species qualified as cosmopolitan, i.e., with multiple well-established outdoors populations outside their native hemisphere (Tables 1-3). Twenty of the 42 cosmopolitan ant species have established populations in all seven of the world's ant-inhabited biogeographic regions (i.e., all except the Antarctic, which ironically has no ants).

I subdivided the 28 cosmopolitan species that were not on Forel's (1911) list into two categories based on a fairly crude evaluation of their degree of geographic spread. Widespread cosmopolitan species (Table 2) have multiple well-established populations in at least five of the world's biogeographic regions: Cardiocondyla mauritanica Forel, 1890, Cardiocondyla minutior Forel, 1899, Cardiocondyla obscurior Wheeler, 1929, Cardiocondyla wroughtonii (Forel, 1890), Hypoponera opaciceps (Mayr, 1887), Hypoponera punctatissima (Roger, 1859), Nylanderia bourbonica (Forel, 1886), Plagiolepis alluaudi Emery, 1894, Pseudoponera stigma (Fabricius, 1804), Strumigenys emmae (Emery, 1890), Strumigenys membranifera Emery, 1869, Strumigenys rogeri Emery, 1890, Technomyrmex difficilis Forel, 1892, and Wasmannia auropunctata (Roger, 1863).

Incipient cosmopolitan species (Table 3) have multiple well-established populations in fewer than five bioregions: Brachyponera chinensis (Emery, 1895), Cardiocondyla venustula Wheeler, 1908, Cerapachys biroi Forel, 1907, Hypoponera eduardi (Forel, 1894), Hypoponera ragusai (Emery, 1894), Leptogenys maxillosa (Smith, 1858), Myrmica rubra (Linnaeus, 1758), Nylanderia flavipes (Smith, 1874), Pheidole teneriffana Forel, 1893, Solenopsis invicta Buren, 1972, Strumigenys hexamera (Brown, 1958), Technomyrmex vitiensis Mann, 1921, Tetramorium insolens (Smith, 1861), and Tetramorium lucayanum Wheeler, 1905.

In addition to 42 cosmopolitan ant species, I listed 20 ant species with only minor spread of outdoor populations outside their native hemisphere: Cardiocondyla tjibodana Karavaiev, 1935, Formica lugubris Zetterstedt, 1838, Monomorium salomonis (Linnaeus, 1758), Monomorium subopacum (Smith, 1858), Myrmica specioides Bondroit, 1918, Nylanderia steinheili (Forel, 1893), Pheidole fervens Smith, 1858, Pheidole moerens Wheeler, 1908, Pseudomyrmex gracilis (Fabricius, 1804), Solenopsis globularia (Smith, 1858), Strumigenys silvestrii Emery, 1906, Syllophopsis sechellensis (Emery, 1894), Tapinoma sessile (Say, 1836), Temnothorax longispinosus (Roger, 1863), Tetramorium pacificum Mayr, 1870, Tetramorium tonganum Mayr, 1870, Tetramorium tsushimae Emery, 1925, and Vollenhovia emeryi Wheeler, 1906 (Table 4). Some of these species appear to be spreading quickly, e.g., T. tsushimae (Reuther, 2009). Other species are known outside their native hemisphere from only a single outdoor site record: C. tjibodana (in Belize; Seifert, 2003), F. lugubris (in Quebec, Canada; Finnegan, 1975), M. subopacum (in Antigua; Wheeler, 1923), M. specioides (in Washington State; Jansen and Radchenko, 2009), N. steinheili (in Mauritius; Wheeler, 1922), P. fervens (in California; Martinez, 1996), Tapinoma sessile (in Hawaii; Buczkowski and Krushelnycky, 2012), T. longispinosus (in Spain; Espadaler and Collingwood, 2001), and T. tonganum (in Brazil; Fowler et al., 1994). In some cases, these single populations may be (or may have been) only temporary.

Discussion

My analyses identified 62 ant species with populations established outside their native range hemisphere. Based on their known world distribution, I classified 42 of these ant species as cosmopolitan, i.e., with multiple well-established outdoor populations outside their native hemisphere (Tables 1-3). Of these 42 cosmopolitan ant species, 35 (83%) are Old World natives and seven (17%) are New World natives. This pattern suggests that Old World species are more likely to be competitively dominant, possibly due to evolving in a more competitive environment. Overall, the highest

number of cosmopolitan ant species were originally native to the Indomalay bioregion (17 species; Tables 1-3) and the lowest number were native to the Nearctic bioregion (only one species; Table 2). Of the 20 ant species with only very minor spread of outdoor populations outside their native hemisphere (Table 4), thirteen (65%) are Old World natives and seven (35%) are New World natives.

Comparing the native ranges of Forel's (1911) cosmopolitans with those of the newer cosmopolitans suggests a shift in the main sources of cosmopolitans. For example, only one of Forel's (1911) 14 cosmopolitans (7%) is native to the Palearctic bioregion, despite the Palearctic having the greatest land area. In contrast, eight of the 28 new cosmopolitans (29%) are native to the Palearctic (Tables 1-3).

Of the 42 cosmopolitan ant species, I consider twelve to be major ecological, agricultural, and/or household pest species. Forel's (1911) list of 14 cosmopolitan ant species (Table 1) included eight of these major pest species (see Introduction). In contrast, my list of 28 additional cosmopolitan ant species (Tables 1 and 2) includes only four additional major pest species: Nylanderia bourbonica (Forel, 1886), Solenopsis invicta Buren, 1972, Technomyrmex difficilis Forel, 1892, and Wasmannia auropunctata (Roger, 1863). The other 24 new cosmopolitans are at most relatively minor pests. Thus, although the new list of cosmopolitan ants is much longer than that of Forel (1911), few of the additions have developed into major pests.

My classification of what constitutes a major pest, however, is not based on quantitative criteria, but instead is largely subjective, based on my experience with the different species and the papers I have read about their impact. All twelve of these major pest species commonly attain high local densities where they can have measurable ecological and/or economic impacts. There are certainly valid arguments for including other ant species on this list. For example, T. bicarinatum can sometimes be a serious agricultural pest and B. chinensis and M. rubra both have painful stings; all three of these species can attain high densities in some places.

In a related problem of categorization, Sarah Lowe, a staff member of the Invasive Species Specialist Group (ISSG) of the International Union for Conservation of Nature (IUCN), asked me in 1997 at a scientific meeting in Suva, Fiji, what I thought were the most harmful exotic ants, for inclusion on a list of 100 of the worst invasive species in the world. I was skeptical about the validity of comparing the relative impact of different ant species, much less comparing the impact of invasive ants with that of invasive mammals, fish, trees, etc. Some ants are enormous agricultural pests, others have a great impact on native species, while still others are important household pests. But Lowe assured me that this publication was a "publicity booklet," simply meant to call attention to exotic species and to IUCN's newly created Global Invasive Species Database. She emphasized this was not to be a list of the 100 worst, but instead 100 examples of harmful invasive species. I suggested six ant species based on my experience at the time: A. gracilipes, L. humile, P. megacephala, S. geminata, S. invicta, and W. auropunctata. In the publication, Lowe et al. (2000) dropped S. geminata because they did not want two species of the same genus. While I would certainly rank S. geminata ahead of A. gracilipes, Lowe et al. (2000) explicitly stated: "Absence from the list does not imply that a species poses a lesser threat." This distinction, however, seems to have been lost in the many dozens of papers that claim species x is one of the 100 worst exotic species, inappropriately citing Lowe et al. (2000) as if this paper were an authoritative primary source founded on definitive research, rather than being a collection of illustrative examples selected based on subjective impressions.

Another problem with categorization is exemplified in a paper by McGlynn (1999), which included a list of 147 ant species that have been “recorded outside their native habitat.” This paper has been a popular source reference regarding exotic ants, cited in the mistaken belief that it represented a comprehensive list of ant species with established exotic populations. McGlynn's (1999) list, however, included a great many ant species that have no known outdoors populations established in locales beyond their native range, e.g., numerous species that Nishida (1994, 2002) listed as intercepted by quarantine

on goods imported into Hawaii, but without any established populations (e.g., Camponotus exiguoguttatus Forel, 1886, Camponotus itoi Forel, 1912, Camponotus obscuripes Mayr, 1879, Crematogaster lineolata (Say, 1836), Formica subpolita Mayr, 1886, Lasius interjectus Mayr, 1866, Pheidole barbata Wheeler, 1908, Pheidole hyatti Emery, 1895, Pheidole noda Smith, 1874, Pheidole punctatissima Mayr, 1870, Carebara affinis (Jerdon, 1851), Polyrhachis argentea Mayr, 1862, Polyrhachis dives Smith, 1857, Polyrhachis femorata Smith, 1858, Ponera coarctata (Latreille, 1802), Prenolepis imparis (Say, 1836) and Prenolepis melanogaster Emery, 1893). In addition, some species on McGlynn's (1999) list have only exotic indoor populations (e.g., Camponotus atriceps (Smith, 1858), Dolichoderus thoracicus (Smith, 1860), Linepithema iniquum (Mayr, 1870), Carebara diversus (Jerdon, 1851) and Solenopsis texana Emery, 1895), and a few were based on site error (e.g., Anoplolepis custodiens (Smith, 1858), Dolichoderus quadripunctatus (Linnaeus, 1771), Gnamptogenys porcata (Emery, 1896), Odontomachus simillimus Smith, 1858 etc.) (Wetterer 2005, 2014c) or identification error (e.g., Cardiocondyla nuda (Mayr, 1866), N. vividula (Nylander, 1846), Pheidole variabilis Mayr, 1876, Brachyponera obscurans (Walker, 1859) etc.) (Seifert 2003). Finally, some species listed actually appear to be native throughout their known range (e.g., Hypoponera elliptica (Forel, 1900), Lasius turcicus Santschi, 1921) (Taylor, 1987;Seifert, 1992).

A complete list of all ant species that have ever been "recorded outside their native habitat" would be much greater than the 147 listed by McGlynn (1999), especially if the list included species simply intercepted in transit. For example, Suarez et al. (2005) listed 232 ant species intercepted by quarantine inspectors in the US. However, Suarez et al. (2005) found that only 28 of these "now occur as established nonnative species in the continental United States, and three species can be considered invasive." I believe that distinguishing these different categories is of vital importance.

Future research plans

I have authored or co-authored papers, reviewing, one species at a time, the known geographic distributions of most cosmopolitan ant species whose taxonomy are well established (Tables 1-3). I am working to review the rest, when the taxonomy can be properly ascertained and specimens with uncertain identities re-examined, often in collaboration with one or more taxonomic experts (e.g., T. simillimum with F. Hita-Garcia). My present list of cosmopolitan ant species is almost certainly incomplete. Taxonomic revisions will probably identify additional cosmopolitan ant species, e.g., one or more Brachymyrmex species appear to be widespread cosmopolitans. Unfortunately, the taxonomy of Brachymyrmex remains very confused.

I am also turning my attention to ant species reported to have exotic populations only within their own native hemisphere. Some of these species have large geographic gaps between their presumed native and exotic populations, e.g., Gnamptogenys triangularis (Mayr, 1887) (MacGown and Wetterer, 2012a) and Pheidole obscurithorax Naves, 1985 (Naves, 1985), so the limits of the known native and exotic ranges can be discerned. For many species, however, distinguishing where the native range ends and the exotic range begins is difficult, e.g., Brachyponera sennaarensis (Mayr, 1862) (Wetterer 2013a) and Strumigenys margaritae Forel, 1893 (MacGown and Wetterer, 2013).

In some cases, species that have been reported as exotic are actually native throughout their known range. Wittenborn and Jeschke (2011) wished to compare characteristics of native versus exotic ant species in North America, but appear to have misclassified numerous ant species as exotics, that are actually native to North America, such as Leptogenys manni (Wheeler, 1923), a species endemic to Florida (Trager and Johnson, 1988).

For example, Wittenborn and Jeschke (2011) considered Gnamptogenys hartmani (Wheeler, 1915), Labidus coecus (Latreille, 1802), Pachycondyla harpax (Fabricius, 1804), and Trachymyrmex jamaicensis (André, 1893) as exotic to North America, but all four have distributions in the southern US that are simply the northern end of continuous native ranges and give no indication that these species are exotic to

Table 1. Forel's (1911) fourteen cosmopolitan ant species. x-date = year first found outside native hemisphere. Bioregions: Af = Afrotropic, Pa = Palearctic, In = Indomalay, Au = Australasia, Oc = Oceania, Na = Nearctic, and Nt = Neotropic. Presumed native range in caps and bold and rest shows presumed exotic range

Species name	Worldwide range							x-date	Major exotic reference
Cardiocondyla emeryi	**AF**	Pa	In	Au	Oc	Na	Nt	1878	Wetterer, 2012d
Pheidole megacephala	**AF**	Pa	In	Au	Oc	Na	Nt	1858	Wetterer, 2012e
Tetramorium caldarium	**AF**	Pa	In	Au	Oc	Na	Nt	1908	Wetterer and Hita Garcia, 2015
Tetramorium simillimum	**AF**	Pa	In	Au	Oc	Na	Nt	1868	Bolton, 1980
Trichomyrmex destructor	Af	**PA**	In	Au	Oc	Na	Nt	1893	Wetterer, 2009b
Monomorium floricola	Af	Pa	**IN**	Au	Oc	Na	Nt	1863	Wetterer, 2010a
Monomorium pharaonis	Af	Pa	**IN**	Au	Oc	Na	Nt	1864	Wetterer, 2010c
Paratrechina longicornis	Af	Pa	**IN**	Au	Oc	Na	Nt	1859	Wetterer, 2008
Tapinoma melanocephalum	Af	Pa	**IN**	Au	Oc	Na	Nt	1793	Wetterer, 2009a
Tetramorium lanuginosum	Af	Pa	**IN**	Au	Oc	Na	Nt	1912	Wetterer, 2010b
Anoplolepis gracilipes	Af	---	**IN**	Au	Oc	Na	Nt	1859	Wetterer, 2005
Tetramorium bicarinatum	Af	Pa	**IN**	**AU**	Oc	Na	Nt	1850	Wetterer, 2009c
Linepithema humile	Af	Pa	In	Au	Oc	Na	**NT**	1858	Wetterer, et al., 2009
Solenopsis geminata	Af	Pa	In	Au	Oc	Na	**NT**	1851	Wetterer, 2011a

Table 2. Fourteen additional widespread cosmopolitan ant species with substantial geographic spread outside their native hemisphere. Symbols and abbreviations as in Table 1.

Species name	Worldwide range							x-date	Major exotic reference
Strumigenys membranifera	**AF**	Pa	In	Au	Oc	Na	Nt	1890	Wetterer, 2011b
Strumigenys rogeri	**AF**	Pa	In	Au	Oc	Na	Nt	1862	Wetterer, 2012a
Plagiolepis alluaudi	**AF**	Pa	In	Au	Oc	Na	Nt	1928	Wetterer, 2014a
Technomyrmex difficilis	**AF**	----	In	Au	Oc	Na	Nt	1986	Wetterer, 2013b
Hypoponera punctatissima	**AF**	**PA**	In	Au	Oc	Na	Nt	1892	Bolton and Fisher, 2011
Cardiocondyla mauritanica	Af	**PA**	In	Au	----	Na	Nt	1967	Wetterer, 2012f
Nylanderia bourbonica	Af	Pa	**IN**	Au	Oc	Na	Nt	1924	Deyrup et al., 2000
Cardiocondyla minutior	Af	----	**IN**	Au	Oc	Na	Nt	1924	Wetterer, 2014b
Cardiocondyla wroughtonii	Af	Pa	**IN**	Au	Oc	Na	Nt	1939	Seifert, 2003
Cardiocondyla obscurior	Af	Pa	**IN**	----	Oc	Na	Nt	1982	Seifert, 2003
Strumigenys emmae	Af	----	In	**AU**	Oc	----	Nt	1890	Wetterer, 2012c
Hypoponera opaciceps	----	Pa	In	Au	Oc	**NA**	Nt	1892	Wilson and Taylor, 1967
Pseudoponera stigma	----	----	In	Au	Oc	Na	**NT**	1858	Wetterer, 2012b
Wasmannia auropunctata	Af	Pa	----	Au	Oc	Na	**NT**	1893	Wetterer, 2013d

Table 3. Fourteen incipient cosmopolitan ant species with several well-established outdoor populations outside their native hemisphere. Symbols and abbreviations as in Table 1.

Species name	Worldwide range							x-date	Major exotic reference
Cardiocondyla venustula	**AF**	----	In	----	Oc	Na	Nt	1906	Seifert, 2003
Leptogenys maxillosa	**AF**	Pa	In	----	----	----	Nt	1861	Roger, 1861
Pheidole teneriffana	**AF**	**PA**	In	----	----	Na	Nt	1930	Wetterer, 2011e
Monomorium salomonis	Af	**PA**	----	----	----	----	Nt	1913	Wheeler and Mann, 1914
Myrmica rubra	----	**PA**	----	----	----	Na	----	1900	Wetterer and Radchenko, 2011
Hypoponera eduardi	Af	**PA**	----	Au	Oc	----	Nt	1914	Bolton and Fisher, 2011
Nylanderia flavipes	----	**PA**	**IN**	----	----	Na	----	1939	Wetterer, 2011c
Brachyponera chinensis	----	**PA**	**IN**	Au	----	Na	----	1932	Nelder et al., 2006
Tetramorium tsushimae	----	**PA**	**IN**	----	----	Na	----	1988	Reuther, 2009
Hypoponera ragusai	Af	Pa	**IN**	Au	Oc	----	Nt	1939	Bolton and Fisher, 2011
Cerapachys biroi	Af	----	**IN**	----	Oc	----	Nt	1930	Wetterer et al., 2012
Technomyrmex vitiensis	Af	Pa	**IN**	**AU**	**OC**	Na	Nt	1987	Bolton, 2007
Solenopsis invicta	----	----	In	Au	----	Na	**NT**	2001	Wetterer, 2013c
Solenopsis globularia	Af	----	----	----	Oc	----	**NT**	1958	Wetterer et al., 2007

Table 4. Twenty ant species with a small number of outdoor populations outside their native hemisphere. Symbols and abbreviations as in Table 1.

Species name	Worldwide range							x-date	Major exotic reference
Tetramorium lucayanum	**AF**	Pa	----	----	----	----	Nt	1904	Wetterer, 2011d
Monomorium subopacum	Af	**PA**	In	----	----	----	Nt	1920	Wheeler, 1923
Formica lugubris	----	**PA**	----	----	----	----	Nt	1973	Finnegan, 1975
Myrmica specioides	----	**PA**	----	----	----	Na	----	<2007	Jansen and Radchenko, 2009
Myrmica scabrinodis	----	**PA**	----	----	----	Na	----	2009	Clark et al., 2011
Vollenhovia emeryi	----	**PA**	**IN**	----	----	Na	----	1986	Wetterer et al., 2015
Strumigenys hexamera	----	**PA**	**IN**	----	----	Na	----	1987	MacGown and Wetterer, 2012b
Cardiocondyla tjibodana	----	**PA**	**IN**	**AU**	----	----	Nt	1997	Seifert, 2003
Pheidole fervens	----	**PA**	**IN**	**AU**	**OC**	Na	----	1995	Martinez, 1996
Tetramorium pacificum	Af	----	**IN**	**AU**	**OC**	Na	----	1950	Creighton, 1950
Tetramorium tonganum	----	Pa	**IN**	**AU**	**OC**	----	Nt	<1994	Fowler et al., 1994
Syllophopsis sechellensis	Af	----	**IN**	**AU**	Oc	----	Nt	2003	Wetterer, in prep.
Tetramorium insolens	Af	Pa	**IN**	**AU**	**OC**	Na	----	1979	Bolton, 1979
Temnothorax longispinosus	----	Pa	----	----	----	**NA**	----	1923	Espadaler and Collingwood, 2001
Tapinoma sessile	----	----	----	----	Oc	**NA**	----	2009	Buczkowski and Krushelnycky, 2012
Pseudomyrmex gracilis	----	Pa	----	----	Oc	**NA**	**NT**	1912	Wetterer, 2010d
Strumigenys silvestrii	----	Pa	In	----	----	Na	**NT**	2001	MacGown et al., 2013
Nylanderia steinheili	Af	----	----	----	----	----	**NT**	1908	Wheeler, 1922
Pheidole moerens	----	----	----	----	Oc	Na	**NT**	2000	Wilson, 2003
Cyphomyrmex minutus	Af	----	----	----	----	----	**NT**	2011	B. Fisher (pers. comm.)

North America (Wetterer 2014c, Wetterer and Snelling 2015).

I eventually plan to make a comprehensive analysis of all ant species with well-established exotic populations, including those that have not spread beyond their native hemisphere. This, however, will take much additional effort in compiling and evaluating specimen records.

More than 100 years ago, Forel (1911) compiled a list of cosmopolitan ants, calling attention to this important group of invasive species, spread around the world by human commerce. Forel (1911) identified most of what remain the dominant tramp ant species today. I hope that my present compilation will prove to be a useful extension of Forel's (1911) prescient work.

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